# H I L G A R D I A

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# CHARACTERS, DISTRIBUTION, AND FOOD PLANTS OF LEAFHOPPER SPECIES IN THAMNOTETTIX GROUP[1]


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## INTRODUCTION

SOME years ago three species (Severin, 1929, 1934)[4] and a biological race (Severin, 1940) of one of these leafhopper species were reported to transmit the California aster-yellows virus. Recently, DeLong and Severin (1945, 1946, 1947*a*, 1947*b*) recorded thirteen additional leafhopper vectors of the virus. The present paper deals with the characters, distribution, and food plants of eight more leafhopper vectors, two of which have been previously mentioned in the literature (Severin, 1934). In a companion paper Severin (1948) discusses the transmission of the virus by these eight leafhopper species.

The genus *Thamnotettix* was erected by Zetterstedt (1840) to include European species, and *Cicada prasina* Fallen was designated as the type. The early American workers placed a large number of American species in this genus as they were described. In recent years several new genera have been described to include certain groups of closely related American species formerly in the genus *Thamnotettix*. The species treated in the present paper have been placed in three genera described by Ball (1936). These are *Idiodonus, Colladonus,* and *Friscananus*. There is little doubt that these species in the three genera are closely related; they may belong to a single genus. The color patterns will usually distinguish them, but the genital structures are similar in both the males and the females of the species concerned. The females usually bear a median sunken spatulate process on the last ventral segment which varies in width, length, and the degree of production beyond the posterior margin in different species. The males may be distinguished by the shape of the style and the length and position of the spine on each side of the caudal margin of the pygofer.

## IDIODONUS HEIDEMANNI (BALL)

*Idiodonus heidemanni* (Ball) is blunt-headed and has a general color of grayish green, sprinkled with minute red spots. It is 4 mm long.

The vertex (fig. 1, *A*) is broad, bluntly produced, and about twice as wide at the base between the eyes as the median length.


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[4] See "Literature Cited" for citations, referred to in the text by author and date.

The vertex and face are pale yellow; the face has several fuscous arcs. The pronotum is pale, dull green; the anterior portion is paler. The scutellum is yellow with an orange spot in each basal angle. The elytra are milky white and subhyaline, with a greenish tint. The entire upper surface and the face are closely dotted with minute, reddish, pepperlike spots.

The last ventral segment of the female (fig. 1, *B*) is roundedly produced and bluntly rounded at the apex. The male plates are rather broad at the base,

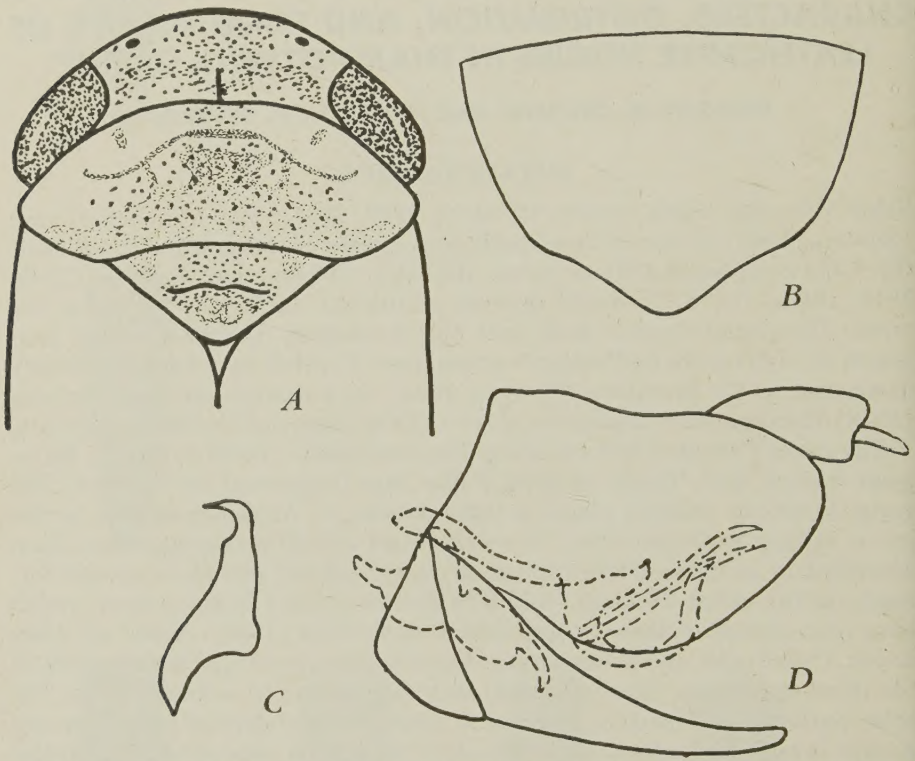


Fig. 1. *Idiodonus heidemanni* (Ball): *A*, dorsal view of head, pronotum, and scutellum; *B*, female last ventral segment; *C*, ventral view of male style; *D*, lateral view of male genitalia.

and roundedly narrowed to form slender, elongated, tapering apices. The male style (fig. 1, *C*) is rather broad at the base and rather short, narrowed to a pointed apex, which is curved outwardly and directed laterally. The aedeagus (fig. 1, *D*) is sicklelike in lateral view, with a pair of long slender processes extending dorsally and caudally from the base of the sickle beyond its apex. The pygofer is rounded without a spine at its apex.

**Breeding Experiments.** Ball (1900) described *Idiodonus heidemanni* (Ball) (= *Thamnotettix heidemanni* Ball) collected from Cerro Summit and Alder, Colorado, both high mountain points. Ball (1911) also described *I. schwartzi* (Ball) (= *T. schwartzi* Ball) from a pair taken at Dewey, Utah, by J. R. Horton, and from one female taken at Ashford, Arizona, by Barber and Schwartz; the latter he received from the United States National Museum.

Ball (1900) described the color of *Idiodonus heidemanni* as grayish green sprinkled with blood-red dots; the detailed color description is as follows:

> The vertex and face pale yellow, sutures and about five short arcs on the front fuscous, pronotum pale olive, the anterior margin lighter, scutellum yellow, an orange spot inside each basal angle. Elytra milky subhyaline with a greenish cast, the black tergum showing through. Whole upper surface and face minutely dotted with blood red.

Ball (1911) described *Idiodonus schwartzi* as smoky cinereous, with two round black spots on the front of the head, and two angled ones on the scutellum; his description is as follows:

> The vertex pale yellow, slightly washed with orange, the ocelli red, a pair of round black spots between them equidistant from the ocelli and each other. Face pale yellow, the sutures dark, a few short smoky arcs on lower part of front. Pronotum cinereous. Scutellum yellow, a triangular black spot just within each basal angle. Elytra cinereous, the costal margin subhyaline, a narrow smoky stripe at apex. Veins of clavus and claval suture pale, veins on corium and a line along the claval suture smoky, emphasized on a line which follows the outer sector omitting its outer branch, and ends in the margin of the third apical cell.

In breeding experiments by the junior author, pairs of recently molted adults were mated, the males fitting the description of *Idiodonus schwartzi*, the females similar except that some had no spots, some 1 black spot, and some the typical 2 spots between the ocelli. Each pair without exception had some offspring with no spots, some with 1 spot, and some with 2 spots, as shown in plate 1, *A* to *H*. Males and females with blood-red dots on the body (plate 1, *I, J, K, L*), and otherwise fitting the description of *I. heidemanni*, were mated. Some of the offspring of each pair failed to show the red spots. Females with acute and rounded heads were mated, each with males of the same type. The offspring of pairs with acute heads had both acute and rounded heads; and the offspring of those with rounded heads likewise had both acute and rounded heads. During the winter most of the adults are brown in color (plate 1, *E, F, G, H*) and during the summer gray forms (plate 1, *A, B, C, D*) predominate. This is true both under natural conditions and under greenhouse conditions. This breeding evidence indicates that we are dealing with color variations of a single species. The priority name which must be given to this species is *Idiodonus heidemanni*.

**Geographical Range.** The detailed occurrence of *Idiodonus heidemanni* is not known, but it is recorded for California and Colorado (Ball, 1900). It probably occurs in other states of the northwestern United States.

**Distribution and Food Plants in California.** The localities in which *Idiodonus heidemanni* was collected and its food plants are as follows:

Los Angeles County: This leafhopper species was commonly taken during the summer of 1919 on Australian saltbush, *Atriplex semibaccata*, near Compton by H. H. P. Severin.

Santa Barbara County: Near Santa Maria and Lompoc, on July 31, 1942, adults were collected in sugar-beet fields by N. W. Frazier.

Napa County: On October 4, 1945, 1 female was captured on an unknown host plant at Larkmead by H. H. P. Severin.

Marin County: Adults were abundant on alkali heath, *Frankenia grandifolia*, October 10, 1946, and July 27, 1947, near San Rafael.

## IDIODONUS KIRKALDYI (BALL)

*Idiodonus kirkaldyi* (Ball) is a pale green to yellowish species with black spots on the vertex, somewhat resembling *Colladonus geminatus* in appearance. It is 3.5 to 4.0 mm long.

The vertex (fig. 2, *A*) is produced and bluntly rounded at the apex. The length at the middle is about the same as the basal width between the eyes.

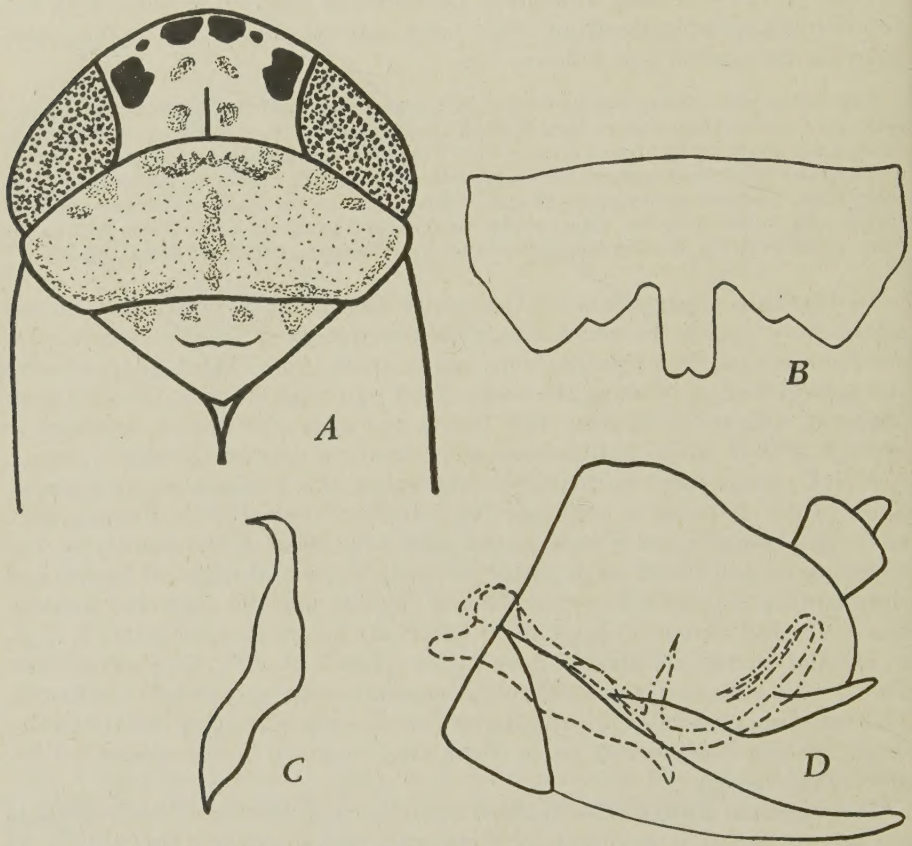


Fig. 2. *Idiodonus kirkaldyi* (Ball): *A*, dorsal view of head, pronotum, and scutellum; *B*, female last ventral segment; *C*, ventral view of male style; *D*, lateral view of male genitalia.

The color of the vertex is creamy yellow with a pair of large, round, black proximal spots at the apex, and a large, round, black spot just back of each ocellus next the eye. A pair of rather large brownish spots are on the base of the vertex; each spot is about equidistant between the eye and the median line. The pronotum is dull yellow to pale brownish, with irregular dark mottling along the anterior margin and on the disk. The scutellum is creamy yellow, with triangular brown spots in the basal angles and a pair of small, round, black spots between them, just back of the anterior margin. The elytra are pale brownish; the costal portion is subhyaline, and the nervures are pale,

usually margined with brown. The elytra appear striped because of a narrow, dark, smoky stripe on the claval area and a wider stripe just inside the outer sector of the corium; the wide stripe extends across the first and second anteapicals and the second apical cell.

The last ventral segment of the female (fig. 2, *B*) is angularly excavated from the prominent lateral angles to the base of a median spatulate process; this process is almost parallel-margined, slightly notched at the apex, and produced beyond the posterior margin of the segment. The male plates are rather broad at the base, then roundedly narrowed to form long, attenuated, tapering apices. The style (fig. 2, *C*) is elongate, only slightly narrowed on the apical fourth, with the apex bent laterally and sharp-pointed. The aedeagus (fig. 2, *D*) is slender, almost parallel-margined, and curves dorsally almost to the anal tube; there it recurves and is divided into a pair of slender processes which extend ventrally. The pygofer bears a spine, which arises on the ventral apical portion and only slightly exceeds the rounded margin of the pygofer.

**Geographical Range.** *Idiodonus kirkaldyi* apparently occurs only in California.

**Distribution and Food Plants in California.** High populations of *Idiodonus kirkaldyi* were collected during the summer and autumn on California sagebrush, *Artemisia californica,* in San Mateo County.

## GEMINATE LEAFHOPPER, COLLADONUS GEMINATUS (VAN DUZEE)

The geminate leafhopper, *Colladonus geminatus* (Van Duzee) is a small, blunt-headed, greenish species with black markings similar to those of *Idiodonus kirkaldyi.* It is 4.5 mm long.

The vertex (fig. 3, *A*) is bluntly and roundedly produced, and almost twice as wide between the eyes at the base as the median length. The ocelli are about one third the distance from the eyes to the apex.

The vertex is yellow in color, with a pair of large triangular black spots on the margin at the apex. An elongate somewhat quadrate black spot is just back of each ocellus. A small brownish spot is just posterior to the inner margin of each of the latter black spots. The pronotum is yellowish anteriorly with a few brown spots along the anterior margin, and the disk is dull greenish brown. The scutellum is dull yellowish, with a median impressed brown line, a pair of round brown spots just in front of it, and a brownish triangular spot about half way from the basal angle to the median line on each side along the anterior margin. The elytra are brown to greenish subhyaline; the nervures are pale except on the apical portion, where they are brown.

The female last ventral segment (fig. 3, *B*) is rounded to the posterior margin, which is somewhat sinuate and distinctly notched either side of a short, rather broad, median spatulate process. This process is produced beyond the posterior margin of the segment and slightly notched at middle. The male plates are broad at the base, then concavely narrowed to rather long acutely pointed apices. The style (fig. 3, *C*) is elongate and rather narrow, more strongly narrowed on the apical sixth. The apex is blunt with a slight toothlike projection on the outer apical margin. The aedeagus (fig. 3, *D*) is slender, almost parallel-margined, with a pair of terminal processes which extend

ventrally from the recurved dorsal portion. The pygofer bears a prominent spine on each side at about the middle of the apical portion.

**Geographical Range.** The geminate leafhopper is quite common and widely distributed in the northwestern United States and in western Canada. It is known to occur in Alaska, British Columbia, Washington, Oregon, California, Colorado, Utah, Wyoming, Montana, and Idaho.

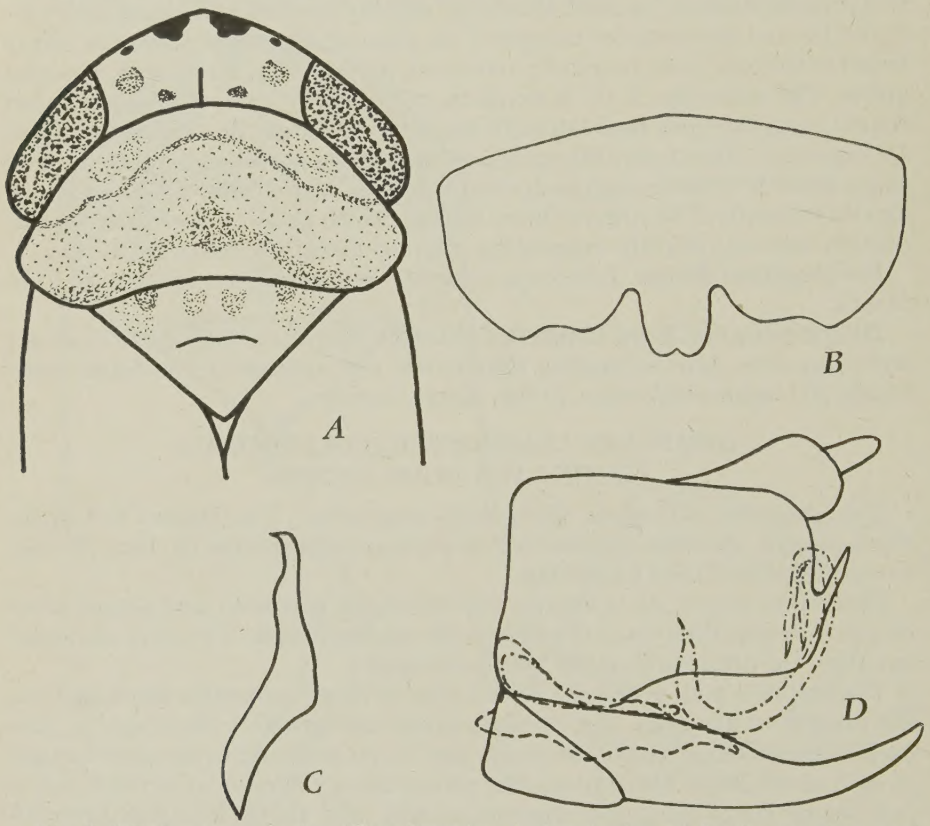


Fig. 3. *Colladonus geminatus* (Van Duzee): *A*, dorsal view of head, pronotum, and scutellum; *B*, female last ventral segment; *C*, ventral view of male style; *D*, lateral view of male genitalia.

**Distribution and Food Plants in California.** The geminate leafhopper is widely distributed in California and has been taken in vegetable fields and on ornamental flowering plants. It has commonly been collected on carrots in the Sacramento and Salinas valleys but rarely on celery, and often on asters in the Salinas Valley (Severin, 1934). Nymphs and adults are abundant on delphiniums and are an efficient vector of the virus to this host plant (Severin, 1942).

## MOUNTAIN LEAFHOPPER, COLLADONUS MONTANUS (VAN DUZEE)

The mountain leafhopper, *Colladonus montanus* (Van Duzee) is a blunt-headed species with a tiny yellow saddle on the commissural line of a pair of black elytra. It is 4.5 mm long.

The vertex (fig. 4, *A*) is bluntly angled and almost twice as wide between the eyes at the base as the median length. The color of the vertex is pale yellow to white, with a darker band on the basal portion between the eyes. The pronotum is pale yellowish except for a darker band on the anterior portion

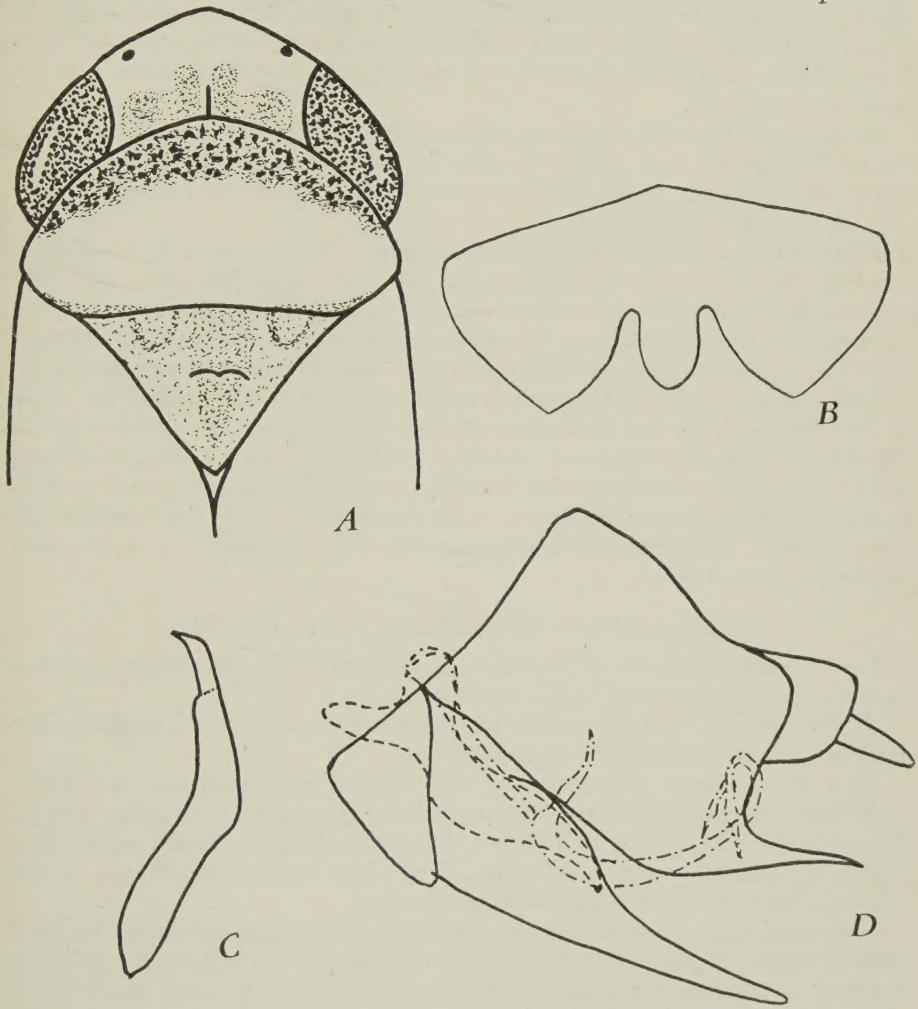


Fig. 4. *Colladonus montanus* (Van Duzee): *A*, dorsal view of head, pronotum, and scutellum; *B*, female last ventral segment; *C*, ventral view of male style; *D*, lateral view of male genitalia.

between the eyes. The scutellum is dark brown to black. The elytra are dark brown or black; the costal half of the corium as far as the apical cell is hyaline with a tiny yellow spot on the corium of the clavus. The face is pale with darker arcs.

The posterior margin of the last ventral segment of the female (fig. 4, *B*) bears a spatulate process at the middle which is produced to the length of the posterior margin and is separated from the broad produced lobes on either

side by a deep U-shaped excavation. The male plates are elongate triangular, with long tapering apices. The male style (fig. 4, *C*) is elongate, only slightly narrowed at the apex. The outer apical margin is pointed. The aedeagus (fig. 4, *D*) extends dorsally, then curves ventrally, forming a pair of slender processes. The pygofer bears a long sharp apical spine on each side, which is directed caudally from the lower portion of the pygofer. This is formed by a deep concave excavation on the dorsal apical portion of the pygofer just beneath the anal tube.

**Geographical Range.** The mountain leafhopper is widely distributed in the Pacific Northwest: it is known to occur in California, Oregon, Washington, Montana, Wyoming, Idaho, Colorado, and Utah in the United States, and in British Columbia in Canada.

**Distribution and Food Plants in California.** The mountain leafhopper is generally distributed in California and has been taken on many different vegetables. During the summer and autumn of 1931 this leafhopper was very abundant in celery fields near Sacramento. Celery was so generally infected with the California aster yellows that it was plowed under (Severin, 1934). Adults captured in the celery and in delphinium fields transmitted the virus to healthy celery; it was thus demonstrated that the insect is a vector of the virus under natural conditions (Severin, 1934, 1942). This leafhopper is one of the most important vectors of the virus to delphinium and breeds on this host plant under natural conditions. A list of economic plants and weeds which serve as food plants of this leafhopper has been published in a previous paper (Severin, 1934).

## COLLADONUS COMMISSUS (VAN DUZEE)

*Colladonus commissus* (Van Duzee) is yellow tinted with orange; it has a bluntly produced head and is 5 to 6 mm long.

The vertex (fig. 5, *A*) is bluntly angled, more than one third longer at the middle than the basal width between the eyes.

The color is straw yellow, tinted with orange, and there are no distinct markings. The pronotum is yellowish, often with a broad triangular spot on the posterior half. The scutellum is yellowish with darker basal angles. The elytra are pale brownish subhyaline, with paler veins except those on the apical portion. The face is pale with faint arcs.

The female last ventral segment (fig. 5, *B*) is strongly produced to form lateral angles, between which the posterior margin is deeply and angularly notched either side of a median rather broad spatulate process, which is not produced to the posterior margin of the segment. The male plates are elongate and triangular. The style (fig. 5, *C*) is elongate and rather narrow, the apical fourth is more narrowed, and the apex bears on the outer margin a rather long-pointed tooth, which extends laterally. The aedeagus (fig. 5, *D*) is rather narrow and curves dorsally, extending almost to the anal tube, where it recurves and divides into two slender terminal processes, which extend ventrally. The pygofer spine, which is on the middle of the caudal portion, is conspicuous.

**Geographical Range.** The known records indicate that *Colladonus commissus* has been taken only in California.

**Distribution and Food Plants in California.** The locality in which *Colladonus commissus* was collected, the food plants on which it was found, and the numbers collected are as follows:

San Mateo County: At Montara, on September 28, 1941, 2 females were collected on California blackberry, *Rubus vitifolius*. On July 31, 1942, 3 males and 9 females were taken on bush lupine, *Lupinus arboreus*, growing in a

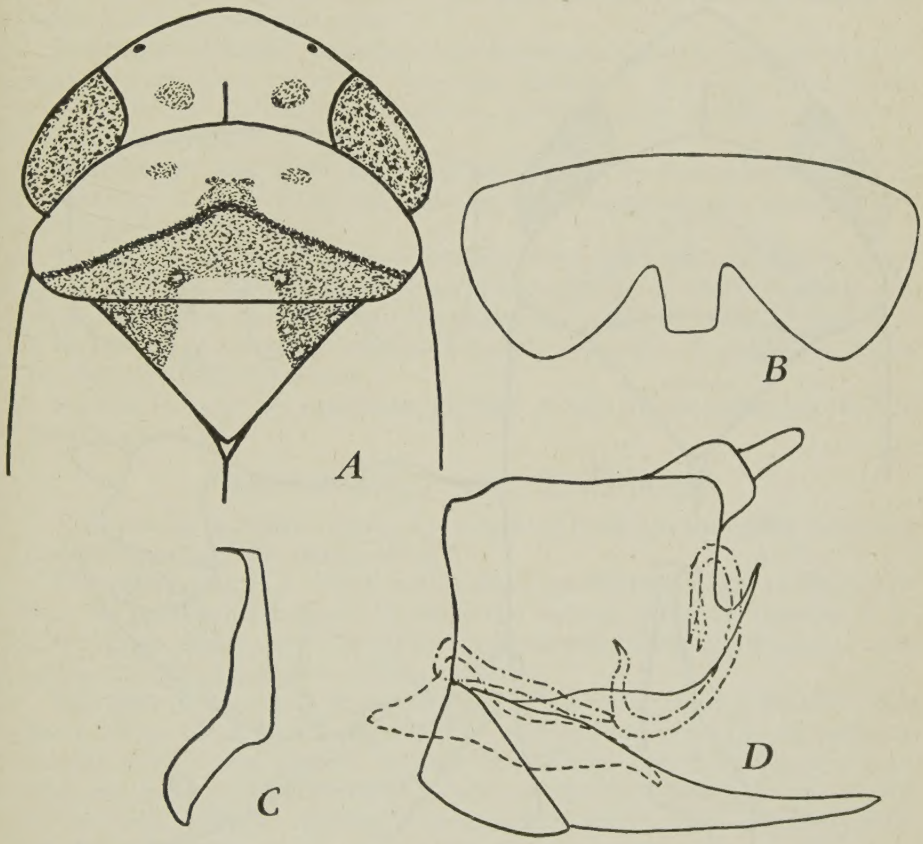


Fig. 5. *Colladonus commissus* (Van Duzee): *A*, dorsal view of head, pronotum, and scutellum; *B*, female last ventral segment; *C*, ventral view of male style; *D*, lateral view of male genitalia.

canyon near Montara. This leafhopper was commonly collected on monkeyflower, *Diplacus aurantiacus*, during the spring, summer, and autumn each year from 1943 to 1945. It was rarely taken on bracken, *Pteridium aquilinum* var. *lanuginosum*, near Montara. On July 25, 1945, 1 female was captured on Allepo pine, *Pinus halepensis*, growing in Sharp Park.

Alameda County: At Berkeley, on August 28, 1942, 1 female was swept from Japanese or Boston ivy, *Parthenocissus tricuspidata*.

Sonoma County: On June 4, 1943, a few adults were collected on an unknown host plant by N. W. Frazier.

## COLLADONUS FLAVOCAPITATUS (VAN DUZEE)

*Colladonus flavocapitatus* (Van Duzee) has a sharply pointed head, which is yellow without markings; the elytra are brown. It is 5.0 to 5.5 mm long.

The vertex (fig. 6, *A*) is produced and angled. The apex is pointed. The median length is more than one half the basal width between the eyes.

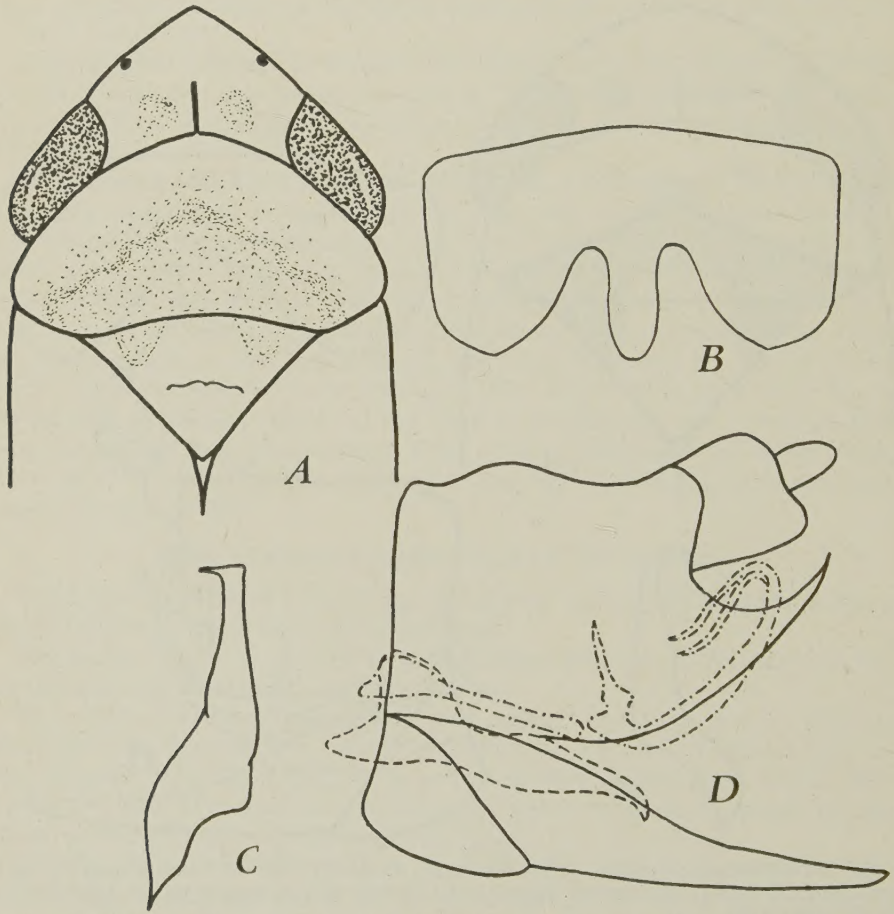


Fig. 6. *Colladonus flavocapitatus* (Van Duzee): *A*, dorsal view of head, pronotum, and scutellum; *B*, female last ventral segment; *C*, ventral view of male style; *D*, lateral view of male genitalia.

The vertex of the male is yellowish, tinted with brown. In the female it is often darker. The pronotum is olive brown, the anterior margin is paler. The scutellum is reddish brown. The elytra are some shade of brown or greenish brown. The face is pale yellow.

The female last ventral segment (fig. 6, *B*) is produced and rather broadly rounded on the outer margins. The posterior margin is deeply excavated either side of a median spatulate process; this process is rounded at the apex and pro-

duced to the length of the posterior margin of the segment. The male plates are elongated triangular, rather broad at the base and rounded, tapering to acute apices. The style (fig. 6, *C*) is elongate, gradually tapered to the apex; the apex is blunt and bears on the outer margin a long toothlike projection, which is directed laterally. The aedeagus (fig. 6, *D*) is directed dorsally and recurved, with a pair of slender processes which extend ventrally. The pygofer bears a long curved apical spine on each side, which is formed by a deep excavation just below the anal tube.

**Geographical Range.** *Colladonus flavocapitatus* is widely distributed in the western portion of the North American continent: it occurs from Alaska through British Columbia and Alberta to Washington, Oregon, California, Idaho, and Colorado.

**Distribution and Food Plants in California.** As determined by N. W. Frazier and J. H. Freitag, the localities and food plants of populations collected are as follows:

Tulare County: Adults were commonly swept from wild gooseberry, *Ribes* sp., growing in General Grant Park, on September 3, 1940; September 3, 1942; September 11, 1943; and September 15, 1944; by N. W. Frazier and J. H. Freitag. Adults were taken on *Ribes cereum* and on *R. roezlii* on August 14, 1947, by H. H. P. Severin.

Sonoma County: On September 11, 1943, 1 male was collected, but the host plant is unknown.

## FRISCANANUS INTRICATUS (BALL)

*Friscananus intricatus* (Ball) has a pointed head and the vertex is without distinct markings. The length is 5 mm.

The vertex (fig. 7, *A*) is pointed at the apex, slightly longer at the middle than the basal width between the eyes. The anterior margin is rounded to the front except at the apex. The elytra contain several irregular reticulate veinlets on the clavus and in the anteapical cells.

The color of the vertex is pale, washed with brown. There is usually a pale band before the eyes. The face is pale with fuscous arcs. The pronotum is usually dark brown with an anterior bow-shaped pale line. The elytra are dark brown with paler nervures, and the irregular reticulations are usually milky white. There is usually an oblique, subhyaline, light area beyond the middle of the costa.

The female last ventral segment (fig. 7, *B*) is concave on the posterior margin, with an angular emargination either side of a median spatulate process, which is rather broad and considerably exceeds the posterior margin in length. The male plates are long and taper to attenuated apices. The style (fig. 7, *C*) is elongate and rather narrow. It is more narrowed on the apical fourth. The apex is bent sharply so as to form a long sharp toothlike projection on the outer margin. The aedeagus (fig. 7, *D*) is narrow and curved dorsally, then recurved ventrally at the anal tube; there it divides into a pair of long slender processes, which are directed ventrally. The pygofer bears a very short pointed spine at about the middle of the caudal margin.

**Geographical Range.** The records of *Friscananus intricatus* indicate that it occurs only in California.

**Distribution and Food Plants in California.** Adult *Friscananus intricatus* were taken in small numbers during the spring, summer, and autumn of 1941 to 1945 on monkey-flower, *Diplacus aurantiacus*, in San Mateo County. At Montara, July 25, 1945, it was occasionally collected on bracken, *Pteridium aquilinum* var. *lanuginosum*.

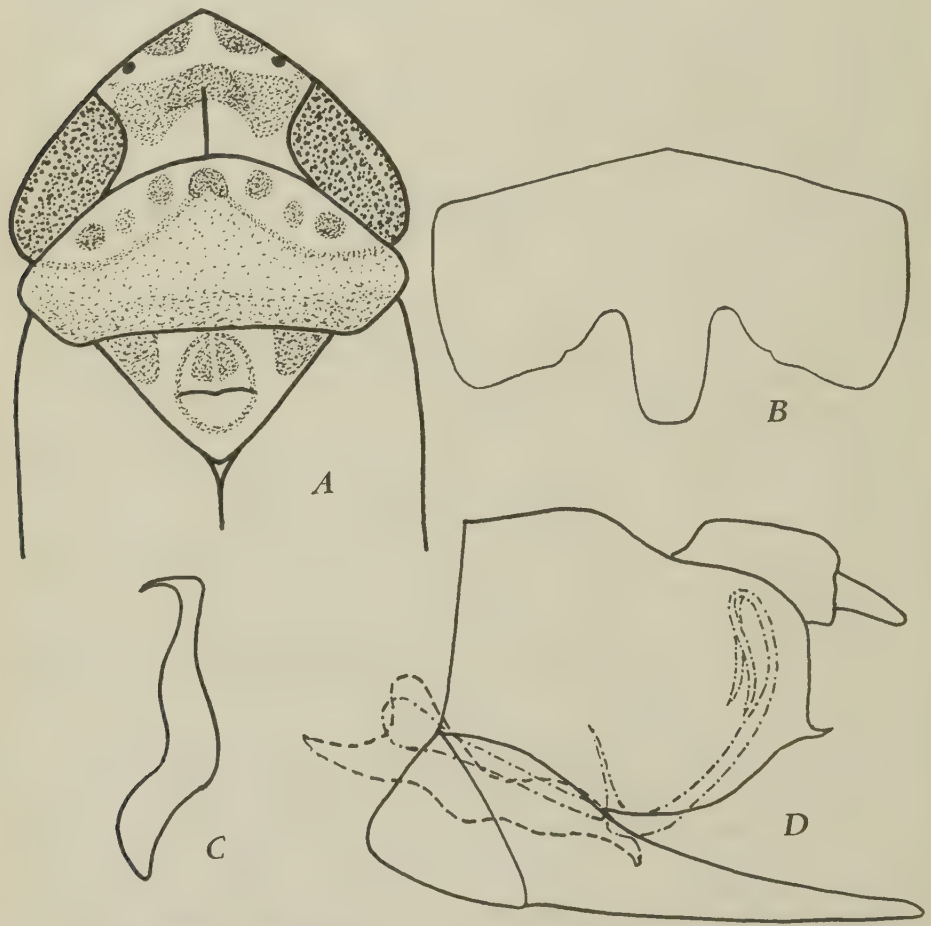


Fig. 7. *Friscananus intricatus* (Ball): *A*, dorsal view of head, pronotum, and scutellum; *B*, female last ventral segment; *C*, ventral view of male style; *D*, lateral view of male genitalia.

## FRISCANANUS RUPINATUS (BALL)

*Friscananus rupinatus* (Ball) resembles *F. intricatus* in having a produced, pointed vertex. In addition it has a bisected black spot at the apex. It is 5 mm long.

The vertex (fig. 8, *A*) is obtusely angled, the apex is rounded, and it is as wide between the eyes at the base as the median length. The elytra do not contain extra reticulate veinlets.

The vertex is orange yellow with a large semicircular black spot on the apex, bisected by the narrow, pale, median line. The pronotum is greenish to reddish brown; the anterior margin is pale. The scutellum is pale yellow; the basal angles are greenish brown. The elytra are greenish subhyaline, washed with brown. The venation is usually inconspicuous. The apices of the claval veins are white, and the veinlets surrounding the apical cells are rusty brown.

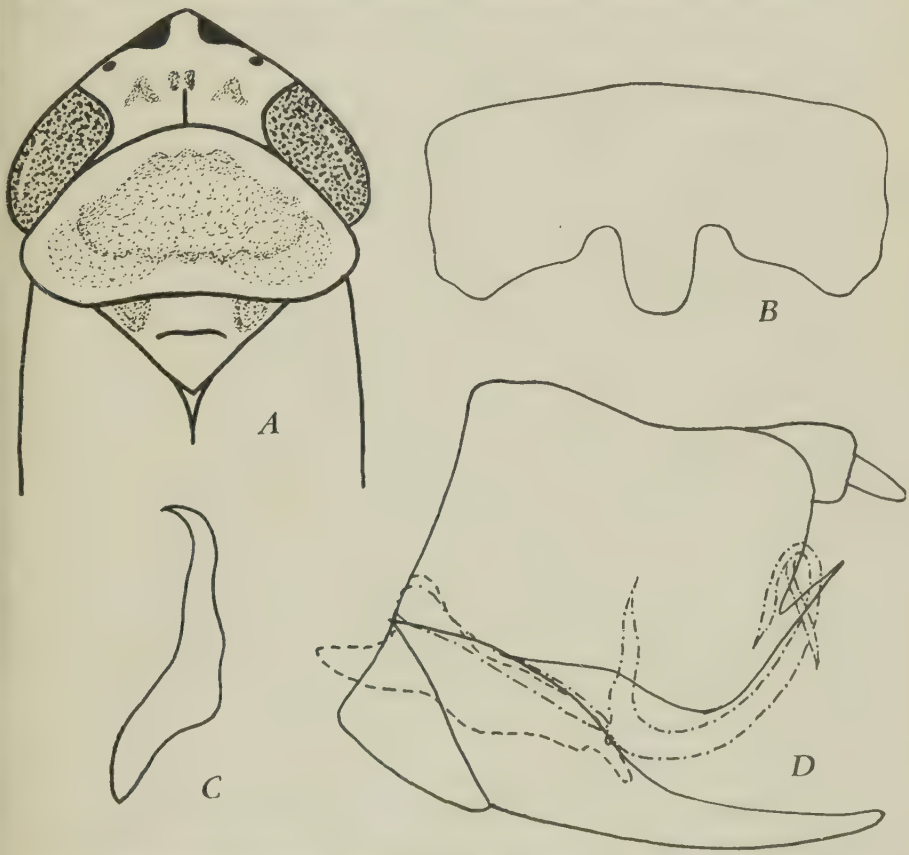


Fig. 8. *Friscananus rupinatus* (Ball): *A*, dorsal view of head, pronotum, and scutellum; *B*, female last ventral segment; *C*, ventral view of male style; *D*, lateral view of male genitalia.

The female last ventral segment (fig. 8, *B*) is concavely rounded on the posterior margin and slightly excavated either side of a rather short, broad median tooth, which extends beyond the posterior margin of the segment. The male plates are long, triangular, and tapered to attenuated apices. The style (fig. 8, *C*) is elongate, somewhat broadened basally, and gradually tapered to a sharply pointed apex, which curves outward. The aedeagus (fig. 8, *D*) is somewhat narrowed on the apical fourth and recurved at the most dorsal point; there it divides into a pair of slender processes, which are directed ventrally. The pygofer bears a conspicuous spine on the posterior margin at about its middle.

**Geographical Range.** According to known records, *Friscananus rupinatus* occurs only in California.

**Distribution and Food Plants in California.** Large populations of *Friscananus rupinatus* were taken during the summer of 1945 on bracken, *Pteridium aquilinum* var. *lanuginosum* near Montara, San Mateo County; but during the autumn, when bracken became dry, few adults were taken. The adults also were captured in small numbers during the spring, summer, and autumn each year from 1941 to 1945 on monkey-flower, *Diplacus aurantiacus.*

## FRISCANANUS RUPINATUS VAR. BRUNNEUS N. VAR.

*Friscananus rupinatus* var. *brunneus* n. var. resembles *F. rupinatus* in form and general appearance but lacks the black spots at the apex of the vertex. It is 4.5–5.0 mm long.

The vertex is bluntly and angularly produced, about one and one third times as wide between the eyes at the middle as the median length in the female, and a little broader proportionately in the male.

The color is pale with reddish-brown markings. The male has two small brown spots at the apex of the vertex, a pale brownish area on basal half between the eyes. Its pronotum is pale, marked with dark brown, with a median pale spot on the anterior margin and a median portion on the posterior margin. Its scutellum is pale with dark-brown spots in the basal angles. Its elytra are subhyaline with brownish markings on clavus and disk. The apical veins and the anterior cross veins of the apical cells are dark brown. Its face is pale with pale fuscous arcs on each side.

The female has a large brownish spot on either side of the apex of the vertex and a rather broad brownish band between the eyes on the basal portion of the vertex. Its pronotum is brown with a median pale light spot on anterior margin. Its scutellum is pale brown except a median pale spot and dark-brown spots in the basal angles. Its elytra are reddish brown, subhyaline; the apical veins are dark brown, the claval and anterior veins are pale; the anterior two thirds have dark-brown areas between the pale veins. Its face is pale with darker arcs than in the male.

Genitalia: The female last ventral segment has a narrow, median, sunken spatulate process as in *Friscananus rupinatus.* The male genitalia are as in *F. rupinatus.*

Holotype female, allotype male, and female paratypes were collected on bracken near Montara, California, by H. H. P. Severin.

**Distribution and Food Plants in California.** Mixed populations of *Friscananus rupinatus* var. *brunneus* and *F. rupinatus* were collected on bracken, *Pteridium aquilinum* var. *lanuginosum,* growing on the Montara Mountains along the Pacific Coast.

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# TRANSMISSION OF CALIFORNIA ASTER-YELLOWS VIRUS BY LEAFHOPPER SPECIES IN THAMNOTETTIX GROUP

HENRY H. P. SEVERIN

# TRANSMISSION OF CALIFORNIA ASTER-YELLOWS VIRUS BY LEAFHOPPER SPECIES IN THAMNOTETTIX GROUP[1]

HENRY H. P. SEVERIN[2]

## INTRODUCTION

According to Ball (1936),[3] the tree- and shrub-inhabiting leafhoppers have been referred in the past to the genus *Thamnotettix,* but are widely separated from the type of the genus and belong to a number of distinct genera. He divided the genus into nine genera.

Some years ago three leafhopper species (Severin, 1929, 1934) and a biological race (Severin, 1940) of one of these species were reported to transmit California aster-yellows virus. In recent papers (Severin, 1945, 1946, 1947*a*, 1947*b*) thirteen more species have been added to the list of vectors of this virus. The present paper deals with nine species and one variety of leafhoppers in the *Thamnotettix* group, two of which have been previously recorded in the literature (Severin, 1934). All were tested for transmission of California aster-yellows virus and some for transmission of the viruses of curly top and Pierce's disease of the grapevine. The companion paper in this issue (DeLong and Severin, 1948) discusses the characters, distribution, and food plants of eight of these leafhopper species.

## METHODS

The cages used and the methods of transferring leafhoppers in a dark chamber were the same as in previous investigations (Severin, 1930, 1931).

The food plants used in maintaining large populations of the geminate leafhopper, *Colladonus geminatus* (Van Duzee), and the mountain leafhopper, *C. montanus* (Van Duzee), have been recorded in previous papers (Severin, 1934, 1942). Infective *Idiodonus heidemanni* (Ball) was reared on diseased celery and asters and noninfective leafhoppers on healthy celery and asters. The other six species and the one variety in the *Thamnotettix* group were collected on their natural host plants. They were not reared on celery and asters, and no attempt was made to breed them on their natural host plants.

## IDIODONUS HEIDEMANNI (BALL)

**Transmission of Virus to Celery.** To determine the efficiency of *Idiodonus heidemanni* (Ball) (= *Thamnotettix heidemanni* Ball) in transmitting California aster-yellows virus, 50 males and 50 females that had completed the nymphal stages on infected celery were transferred singly to healthy celery plants. As table 1 shows, 12 per cent of the males and 20 per cent of the females caused infections.

A comparison was made of the transmission of the virus by 25 lots each of 5, 10, and 20 males and females which had completed the nymphal stages on

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[3] See "Literature Cited" for citations, referred to in the text by author and date.

diseased celery. The lots of 5 were kept on the first set of healthy celery plants to which they were transferred. With the lots of 10 and 20 leafhoppers, if symptoms developed on a plant, the lot on that plant was transferred to another healthy celery plant. If there were no symptoms, some lots were kept on the first healthy celery plant during adult life; others were changed monthly to successive healthy plants until the last adult died. These results appear in table 1.

TABLE 1

TRANSMISSION OF VIRUS BY VARYING NUMBERS OF *Idiodonus heidemanni* TO SUCCESSIVE HEALTHY CELERY PLANTS

| Number of adults in each lot | Number of lots | First set of celery | | | Second set of celery | | | Third set of celery | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Plants inoculated | Plants infected | Per cent infected | Plants inoculated | Plants infected | Per cent infected | Plants inoculated | Plants infected | Per cent infected |
| 1 male | 50 | 50 | 6 | 12 | .. | .. | .. | .. | .. | .. |
| 1 female | 50 | 50 | 10 | 20 | .. | .. | .. | .. | .. | .. |
| 5 males | 25 | 25 | 5 | 20 | .. | .. | .. | .. | .. | .. |
| 5 females | 25 | 25 | 8 | 32 | .. | .. | .. | .. | .. | .. |
| 10 males | 25 | 25 | 18 | 72 | 13 | 4 | 31 | 2 | 1 | 50 |
| 10 females | 25 | 25 | 16 | 64 | 16 | 10 | 63 | 6 | 3 | 50 |
| 20 males | 25 | 25 | 19 | 76 | 22 | 12 | 55 | 10 | 4 | 40 |
| 20 females | 25 | 25 | 16 | 64 | 20 | 17 | 85 | 14 | 5 | 36 |

| Number of adults in each lot | Number of lots | Fourth set of celery | | | Fifth set of celery | | | Total | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Plants inoculated | Plants infected | Per cent infected | Plants inoculated | Plants infected | Per cent infected | Plants inoculated | Plants infected | Per cent infected |
| 1 male | 50 | .. | .. | .. | .. | .. | .. | 50 | 6 | 12 |
| 1 female | 50 | .. | .. | .. | .. | .. | .. | 50 | 10 | 20 |
| 5 males | 25 | .. | .. | .. | .. | .. | .. | 25 | 5 | 20 |
| 5 females | 25 | .. | .. | .. | .. | .. | .. | 25 | 8 | 32 |
| 10 males | 25 | 1 | 0 | 0 | .. | .. | .. | 41 | 23 | 56 |
| 10 females | 25 | 2 | 0 | 0 | .. | .. | .. | 49 | 29 | 59 |
| 20 males | 25 | 1 | 0 | 0 | 1 | 0 | 0 | 59 | 35 | 59 |
| 20 females | 25 | 8 | 5 | 63 | 4 | 1 | 25 | 71 | 44 | 62 |

Table 1 shows that the relation between the percentages of infection caused by males and females, and by lots of 10 and 20, was not constant in the first four sets of celery plants. But the total percentages of infections caused by single males, and by lots of 5, 10, and 20 males, were lower than those of the females. In the lots of 10 and 20, the females inoculated more plants and lived longer than the males. There was a progressive increase in the total percentages of infections with lots of 5, 10, and 20 adults. Thus the number of leafhoppers plays an important role in the transmission of the virus to celery plants.

**Transmission of Virus to Asters.** Fifty infective male and 75 female *Idiodonus heidemanni* were kept singly on healthy asters until symptoms developed, or during adult life if no symptoms appeared. Fourteen per cent of the males and 8 per cent of the females (table 2), an average of 13 per cent, transmitted the virus to asters, as compared with an average of 16 per cent to celery (table 1).

An experiment was conducted with lots of 5, 10, and 20 males and females to determine the percentages of transmission of the virus to successive sets of healthy asters. Each lot of infective adults was kept on a healthy aster until symptoms of the disease appeared and then was transferred to another healthy aster. If no symptoms developed, the surviving adults were changed to successive asters at irregular intervals until the last adult died. The results obtained appear in table 2.

TABLE 2

TRANSMISSION OF VIRUS BY VARYING NUMBERS OF *Idiodonus heidemanni* TO SUCCESSIVE HEALTHY ASTERS

| Number of adults in each lot | Number of lots | First set of asters | | | Second set of asters | | |
|---|---|---|---|---|---|---|---|
| | | Plants inoculated | Plants infected | Per cent infected | Plants inoculated | Plants infected | Per cent infected |
| 1 male | 50 | 50 | 7 | 14 | .. | .. | .. |
| 1 female | 75 | 75 | 6 | 8 | . | .. | .. |
| 5 males | 20 | 20 | 1 | 5 | .. | .. | .. |
| 5 females | 20 | 20 | 15 | 75 | 14 | 3 | 21 |
| 10 males | 10 | 10 | 4 | 40 | 6 | 0 | 0 |
| 10 females | 10 | 10 | 9 | 90 | 10 | 5 | 50 |
| 20 males | 20 | 20 | 6 | 30 | 4 | 1 | 25 |
| 20 females | 23 | 23 | 11 | 48 | 16 | 3 | 19 |

| Number of adults in each lot | Number of lots | Third set of asters | | | Total | | |
|---|---|---|---|---|---|---|---|
| | | Plants inoculated | Plants infected | Per cent infected | Plants inoculated | Plants infected | Per cent infected |
| 1 male | 50 | .. | .. | .. | 50 | 7 | 14 |
| 1 female | 75 | .. | .. | .. | 75 | 6 | 8 |
| 5 males | 20 | .. | .. | .. | 20 | 1 | 5 |
| 5 females | 20 | 4 | 2 | 50 | 38 | 20 | 53 |
| 10 males | 10 | 4 | 0 | 0 | 20 | 4 | 20 |
| 10 females | 10 | 7 | 1 | 14 | 27 | 15 | 56 |
| 20 males | 20 | 1 | 1 | 100 | 25 | 8 | 32 |
| 20 females | 23 | 4 | 2 | 50 | 43 | 16 | 37 |

As table 2 shows, the total percentages of infections of the three sets of asters did not increase progressively with lots of 5, 10, and 20 adults: higher percentages of infections were obtained with lots of 5 and 10 adults than with lots of 20 adults. The total percentages of infections were higher with lots of 5, 10, and 20 females than with the males.

**Transmission of Virus to Two Host Plants.** Transmission of California aster-yellows virus to celery alternating with aster, and to asters alternating with celery, by lots of 20 and 40 male *Idiodonus heidemanni*, was compared. The first and second sets of plants were each exposed to the leafhoppers for a period of 3 days and the third plant during adult life of the insects.

Table 3 shows that when the first sets of celery and asters were exposed to lots of 20 and 40 males for three days, 4 of 20 celery plants and 2 of 20 asters were infected. When the second set of celery plants was exposed to the same number of leafhoppers during adult life, 17 of 20 plants were infected. When

asters alternated with celery, it is evident from table 3, celery was more readily infected than asters.

**Retention of Virus by Single Adults.** Virus retention was determined with single adult *Idiodonus heidemanni* that had transmitted the virus to celery

TABLE 3

TRANSMISSION OF VIRUS TO SUCCESSIVE SETS OF TWO HOST PLANTS BY 10 LOTS EACH OF 20 OR 40 MALE *Idiodonus heidemanni*

| Test no. and plants tested | 20 adults per lot | | | 40 adults per lot | | |
|---|---|---|---|---|---|---|
| | Period of inoculation, days | Plants inoculated | Plants infected | Period of inoculation, days | Plants inoculated | Plants infected |
| Test 1: | | | | | | |
| First set of celery | 3 | 10 | 2 | 3 | 10 | 2 |
| First set of asters | 3 | 10 | 0 | 3 | 10 | 2 |
| Second set of celery | 21–59 | 10 | 8 | 15–60 | 10 | 9 |
| Test 2: | | | | | | |
| First set of asters | 3 | 10 | 1 | 3 | 10 | 2 |
| First set of celery | 3 | 10 | 2 | 3 | 10 | 6 |
| Second set of asters | 23–34 | 10 | 1 | 7–18 | 10 | 1 |

TABLE 4

TRANSMISSION OF VIRUS TO CELERY AND ASTERS BY VARYING NUMBERS OF *Idiodonus kirkaldyi*

| Plant and number of adults in each lot | Number of lots | Plants inoculated | Plants infected | Per cent infected |
|---|---|---|---|---|
| Celery: | | | | |
| 1 male | 50 | 50 | 0 | 0 |
| 1 female | 50 | 50 | 0 | 0 |
| 4 females | 1 | 7 | 2 | 29 |
| 5 males | 3 | 3 | 0 | 0 |
| 5 females | 3 | 3 | 0 | 0 |
| 10 males | 1 | 1 | 0 | 0 |
| 10 females | 3 | 1 | 0 | 0 |
| 20 males | 1 | 1 | 0 | 0 |
| 25 males | 1 | 5 | 0 | 0 |
| Aster: | | | | |
| 1 male | 11 | 11 | 0 | 0 |
| 1 female | 14 | 14 | 0 | 0 |
| 5 males | 2 | 2 | 0 | 0 |
| 5 females | 2 | 2 | 0 | 0 |
| 10 males | 1 | 1 | 0 | 0 |
| 10 females | 1 | 1 | 0 | 0 |
| 20 males | 1 | 1 | 0 | 0 |

in tests of vector efficiency. After a leafhopper had produced the first infection, it was transferred daily to healthy asters during adult life. One male infected the first 2 successive asters, retaining the virus for 11 days after producing the first infection. The incubation period of the disease in the first aster is not included in the retention of the virus, since the adult was able to acquire the virus again. The longevity of the male was 67 days. Two males and 2 females produced only 1 infection in the first aster.

**Attempt to Transmit Curly-Top Virus.** Because the beet leafhopper, *Eutettix tenellus* (Baker), was originally described in the genus *Thamnotettix,* a large number of tests were made to determine whether *Idiodonus heidemanni,* also formerly placed in the genus *Thamnotettix,* was a victor of the curly-top virus. All attempts to transmit curly-top virus to healthy sugar-beet seedlings were failures.

## IDIODONUS KIRKALDYI (BALL)

*Idiodonus kirkaldyi* (Ball) (= *Thamnotettix kirkaldyi* Ball) (plate 1, *A, B*) is an inefficient vector of California aster-yellows virus. The leafhoppers tested were collected from California sagebrush, *Artemisia californica.* One lot of 4 adults was kept on diseased celery for 66 days and then was transferred every week to successive healthy celery plants until the last adult died. Two of 7 plants inoculated were infected. Fifty males and 50 females tested singly on healthy celery produced no infection. Lots of 5, 10, 20, and 25 males or females which were kept on diseased celery from 10 to 14 days, failed to transmit the virus to healthy celery plants (table 4). The virus was not transmitted from infected to healthy asters by varying numbers of adults (table 4).

## GEMINATE LEAFHOPPER, COLLADONUS GEMINATUS (VAN DUZEE)

The geminate leafhopper, *Colladonus geminatus* (Van Duzee) (= *Thamnotettix geminatus* Van Duzee), was previously reported (Severin, 1934) as a vector of the California aster-yellows virus. In a later investigation (Severin, 1942), this leafhopper species was demonstrated to be one of the most important vectors of the virus to perennial delphiniums, and was shown to breed on this host plant under natural conditions.

The number of infections induced by varying numbers of adults has been reported in two previous papers (Severin, 1934, 1942). The transmission of the virus to celery averaged 14 per cent, but no infections were obtained with 182 asters inoculated. Twenty-five lots of 50 males each were used to inoculate asters; and 4 of 50 asters were infected, or 8 per cent (Severin, 1942).

**Transmission of Virus to Celery and Asters.** To determine the efficiency of the geminate leafhopper in transmitting the California aster-yellows virus to celery, 100 males and 100 females that had completed the nymphal stages on diseased celery were transferred singly to healthy celery plants. Two males and 3 females, or 3 per cent, produced infections.

Twelve lots of 20 males were kept on diseased celery for 5, 10, or 15 days, and then each lot was transferred to 37, 32, or 27 successive healthy celery plants. The average number of infections caused by lots of 20 adults was 2.4, 1.5, and 2.4, with exposures of 5, 10, and 15 days, respectively.

Another experiment was undertaken with asters as the host plant. Three hundred males and 300 females that had completed the nymphal stages on naturally infected asters and on experimentally infected asters and celery, were transferred singly to healthy asters. Not a single infection was obtained.

As reported in a previous paper (Severin, 1934), the geminate leafhopper was collected on asters under natural conditions; but a high mortality occurred on small asters in the greenhouse when the adults were transferred

from large asters in the field. It was found that the adults fed on small healthy asters died within a week. Nymphs lived longer than adults, and sometimes the nymphs acquired the winged stage on large asters.

**Latent Period of Virus in Adults.** The latent period of California aster-yellows virus in the geminate leafhopper was determined with 8 lots of single previously noninfective males and 11 lots of 100 males. After 1 day on an

TABLE 5

LATENT PERIOD OF VIRUS IN ADULT GEMINATE LEAFHOPPER, *Colladonus geminatus*, WITH CELERY AS THE HOST PLANT

| Lot no. | Number of adults | Days on infected celery | Successive plants inoculated | Plants infected | Per cent infected | Days on which successive infections occurred, including initial day on infected celery | Adults alive at end of 42 days |
|---|---|---|---|---|---|---|---|
| 1* | 1 | 1 | 41 | 1 | 3 | 31 | 1 |
| 9 | 100 | 1 | 41 | 8 | 20 | 18, 26, 31, 34, 36, 39, 41, 42 | 62 |
| 10 | 100 | 1 | 41 | 12 | 29 | 21, 31, 32, 33, 34, 35, 36, 37, 38, 39, 40, 41 | 75 |
| 11 | 100 | 1 | 41 | 8 | 20 | 23, 26, 27, 28, 30, 32, 39, 41 | 62 |
| 12 | 100 | 1 | 41 | 7 | 17 | 24, 25, 26, 27, 28, 29, 30 | 62 |
| 13 | 100 | 1 | 41 | 2 | 5 | 27, 37 | 37 |
| 14 | 100 | 1 | 41 | 13 | 32 | 27, 28, 30, 31, 32, 34, 35, 36, 37, 38, 39, 41, 42 | 48 |
| 15 | 100 | 1 | 41 | 9 | 22 | 31, 32, 34, 35, 36, 37, 38, 39, 42 | 69 |
| 16 | 100 | 1 | 41 | 5 | 1 | 32, 34, 35, 39, 42 | 15 |
| 17 | 100 | 1 | 41 | 3 | 7 | 33, 37, 42 | 57 |
| 18 | 100 | 1 | 41 | 5 | 1 | 36, 37, 38, 39, 41, 42 | 69 |
| 19 | 100 | 1 | 41 | 6 | 2 | 36, 37, 39, 41, 42 | 48 |
| 20 | 20 | 5 | 37 | 2 | 6 | 22, 23 | 8 |
| 21 | 20 | 5 | 37 | 1 | 3 | 22 | 10 |
| 22 | 20 | 5 | 37 | 1 | 3 | 23 | 9 |
| 23 | 20 | 5 | 37 | 3 | 8 | 26, 30, 34 | 10 |
| 24 | 20 | 5 | 37 | 2 | 6 | 27, 31 | 7 |
| 25 | 20 | 10 | 32 | 1 | 3 | 17 | 7 |
| 26 | 20 | 10 | 32 | 1 | 3 | 33 | 9 |
| 27 | 20 | 15 | 27 | 2 | 7 | 20, 29 | 10 |
| 28 | 20 | 15 | 27 | 2 | 7 | 23, 33 | 11 |
| 29 | 20 | 15 | 27 | 1 | 4 | 31 | 5 |
| 30 | 20 | 15 | 27 | 1 | 4 | 33 | 8 |
| 31 | 20 | 15 | 27 | 1 | 4 | 38 | 20 |

* Lots 2 to 8 were single-insect tests; no infections were obtained with them.

infected celery plant, the adults were transferred daily to successive healthy celery plants throughout a period of 41 days. The virus latent period in 1 male was 31 days, as appears in table 5. Seven lots of single adults kept on diseased celery plants for 1 day and then transferred daily to healthy celery during 41 days failed to cause infections, but 2 adults kept on healthy celery produced infections after 54 and 90 days (not included in table 5). The minimum latent period in 11 lots of 100 males ranged from 18 to 36 days.

**Attempts to Transmit the Viruses of Curly Top and Pierce's Disease of the Grapevine.** In discussing the number of leafhopper vectors of the California aster-yellows virus, plant pathologists have asked repeatedly whether any of these leafhoppers transmit the viruses of curly top and Pierce's disease of the grapevine. All efforts to transmit the curly-top virus by means of the geminate leafhopper were failures. The geminate leafhopper also failed to

transmit the virus of Pierce's disease to healthy wild grapevine seedlings and to California common or Chilean alfalfa; and from alfalfa dwarf to healthy wild grapevine seedlings and healthy alfalfa.

## MOUNTAIN LEAFHOPPER, COLLADONUS MONTANUS (VAN DUZEE)

The mountain leafhopper, *Colladonus montanus* (Van Duzee) (= *Thamnotettix montanus* Van Duzee), has been previously reported as a vector of the California aster-yellows virus (Severin, 1934). This leafhopper is an efficient vector of the virus to perennial delphinium and breeds on this host plant under natural conditions (Severin, 1942).

The number of infections produced by lots of 5, 10, and 20 adults has been published in a previous paper (Severin, 1934). A total of 464 celery plants and 412 asters were inoculated; 121 celery plants and 12 asters were infected, or 26 and 3 per cent, respectively.

**Transmission of Virus to Celery and Asters.** Fifty males and 50 females that had completed the nymphal stages on diseased celery were tested singly on healthy celery plants to determine the efficiency of the mountain leafhopper in transmitting the California aster-yellows virus. Three males and 8 females, or 11 per cent, caused infections.

Thirteen lots of 20 males kept on infected celery for 1 day and then transferred to healthy celery for 41 days caused no infections. With exposures of 5, 10, and 15 days to infected celery, the average number of infections produced by 13 lots of 20 adults was 4, 1.3, and 3, respectively. One lot of 20 adults kept on diseased celery for 5 days and 2 lots for 10 days failed to transmit the virus to healthy celery plants.

The first experiment was repeated with asters as a host plant. Fifty males and 50 females reared during all nymphal stages on naturally infected asters, and on experimentally infected asters and celery, were transferred singly to healthy asters. No infections were produced. The longevity of the adults on asters ranged from 2 to 15 days, with an average of 4.3 days.

**Latent Period of Virus in Adults.** The latent period of the California aster-yellows virus in the mountain leafhopper was determined with 8 lots of single previously noninfective males and 10 lots of 100 males. All lots were kept on diseased celery plants for 1 day and then were transferred daily to successive healthy celery plants for 41 days. As shown in table 6, the latent periods of the virus in 2 single males were 23 and 31 days. Six lots of single males failed to transmit the virus. The minimum latent period of the virus in 10 lots of 100 males ranged from 8 to 40 days. The number of infections produced by each lot and the number of adults alive at the end of 42 days appear in table 6.

**Retention of Virus.** The retention of the California aster-yellows virus in the mountain leafhopper was determined with single males and females that had transmitted the virus in testing the efficiency of virus transmission by this vector. Each leafhopper was kept on a healthy celery plant until the latter showed symptoms, then the insect was transferred to successive healthy celery plants throughout its adult life. Two males and 1 female produced only the initial infection.

TABLE 6

LATENT PERIOD OF VIRUS IN ADULT MOUNTAIN LEAFHOPPER, *Colladonus montanus*, WITH CELERY AS THE HOST PLANT

| Lot no. | Number of adults | Days on infected celery | Successive plants inoculated | Plants infected | Per cent infected | *Days on which successive infections occurred | Adults alive at end of 42 days |
|---|---|---|---|---|---|---|---|
| 1 | 1 | 1 | 41 | 1 | 3 | 23 | 1 |
| 2 | 1 | 1 | 41 | 1 | 3 | 31 | 1 |
| 3 | 100 | 1 | 41 | 7 | 17 | 8, 11, 18, 28, 37, 39, 41 | 42 |
| 4 | 100 | 1 | 47 | 11 | 27 | 15, 16, 17, 20, 22, 26, 27, 29, 32, 35, 41 | 57 |
| 5 | 100 | 1 | 47 | 8 | 20 | 20, 35, 36, 37, 38, 40, 41, 42 | 45 |
| 6 | 100 | 1 | 41 | 3 | 7 | 20, 29, 32 | 40 |
| 7 | 100 | 1 | 41 | 9 | 22 | 23, 25, 26, 28, 30, 33, 35, 36, 41 | 78 |
| 8 | 100 | 1 | 41 | 13 | 32 | 24, 26, 27, 28, 29, 30, 31, 32, 34, 35, 37, 38, 42 | 61 |
| 9 | 100 | 1 | 41 | 11 | 27 | 26, 29, 30, 31, 32, 33, 34, 35, 38, 40, 42 | 60 |
| 10 | 100 | 1 | 41 | 3 | 7 | 30, 32, 35 | 15 |
| 11 | 100 | 1 | 41 | 1 | 3 | 30 | 4 |
| 12 | 100 | 1 | 41 | 2 | 5 | 40, 42 | 73 |
| 13 | 20 | 5 | 37 | 3 | 8 | 22, 32 | 17 |
| 14 | 20 | 5 | 37 | 9 | 3 | 23, 27, 29, 34, 35, 36, 38, 40, 42 | 6 |
| 15 | 20 | 5 | 37 | 2 | 6 | 23, 24 | 14 |
| 16 | 20 | 5 | 37 | 2 | 6 | 33, 36 | 8 |
| 17 | 20 | 10 | 32 | 1 | 3 | 19 | 15 |
| 18 | 20 | 10 | 32 | 1 | 3 | 27 | 19 |
| 19 | 20 | 10 | 32 | 1 | 3 | 32, 35 | 14 |
| 20 | 20 | 15 | 27 | 3 | 1 | 19, 30, 36 | 17 |
| 21 | 20 | 15 | 27 | 3 | 1 | 28, 38, 42 | 16 |
| 22 | 20 | 15 | 27 | 4 | 2 | 29, 30, 34, 37 | 20 |
| 23 | 20 | 15 | 27 | 4 | 2 | 29, 32, 35, 36 | 17 |
| 24 | 20 | 15 | 27 | 3 | 1 | 29, 39, 41 | 14 |
| 25 | 20 | 15 | 27 | 1 | 3 | 38 | 20 |

* Days are numbered from the initial day on infected celery.

TABLE 7

TRANSMISSION OF VIRUS TO CELERY AND ASTERS BY VARYING NUMBERS OF *Colladonus commissus*

| Plant and number of adults in each lot | Number of lots | Plants inoculated | Plants infected | Per cent infected |
|---|---|---|---|---|
| Celery: | | | | |
| 1 male | 50 | 50 | 14 | 28 |
| 1 female | 50 | 50 | 24 | 48 |
| 10 males | 1 | 13 | 9 | 69 |
| 20 males | 1 | 9 | 2 | 22 |
| 25 males | 3 | 24 | 6 | 25 |
| 25 females | 2 | 56 | 16 | 28 |
| Asters: | | | | |
| 1 male | 1 | 1 | 0 | 0 |
| 1 female | 8 | 8 | 0 | 0 |
| 5 females | 5 | 5 | 1 | 20 |

**Attempts to Transmit the Viruses of Curly Top and Pierce's Disease of the Grapevine.** The mountain leafhopper failed to transmit curly-top virus. It also failed to transmit the virus of Pierce's disease to healthy wild grapevine seedlings and to California common or Chilean alfalfa; and from alfalfa dwarf to healthy wild grapevine seedlings or to healthy alfalfa.

## COLLADONUS COMMISSUS (VAN DUZEE)

*Colladonus commissus* (Van Duzee) (= *Thamnotettix commissus* Van Duzee) (plate 1, *C, D,*) was collected on monkey-flower, *Diplacus aurantiacus.*

**Tranmission of Virus to Celery.** The efficiency of *Colladonus commissus* in transmitting the California aster-yellows virus was determined with single adults, each transferred from a diseased to a healthy celery plant. Table 7 shows that 14 to 50 males and 24 of 50 females caused infections of celery plants.

TABLE 8

RETENTION OF VIRUS BY SINGLE ADULT *Colladonus commissus* WITH CELERY AS THE HOST PLANT

| Days on first plant before symptoms developed | Plants inoculated after first infection | Plants infected after first infection | Per cent infected after first infection | Days after first infection on which successive infections occurred | Longevity of adults, days |
|---|---|---|---|---|---|
| 23 | 24 | 12 | 50 | 3, 4, 5, 8, 9, 10, 12, 13, 14, 15, 18, 27 | 47 |
| 21 | 39 | 3 | 8 | 2, 4, 6 | 60 |

Lots of 10 to 25 males or females were transferred from diseased to successive healthy celery plants weekly. Table 7 shows the number of infections produced by each lot of leafhoppers.

To determine whether a longer period of exposure to healthy celery plants is a factor in the transmission of the virus, a male and a female were transferred singly from diseased to successive healthy celery plants every month during adult life. The male infected 2 of 3 plants and the female 3 of 4 plants.

**Transmission of Virus to Asters.** No infections were obtained with 9 adults tested singly on asters. Five lots of 5 adults transmitted California aster-yellows virus to 1 of 5 asters (table 7).

**Retention of Virus by Single Adults.** The retention of California aster-yellows virus by *Colladonus commissus* was determined with single adults that had transmitted the virus in tests of vector efficiency. After the first infection of celery, the leafhopper was transferred daily to successive healthy celery plants during adult life. One female retained the virus for 27 days after symptoms developed on the first plant and caused 12 infections, as appears in table 8. Another female retained the virus for 6 days and produced 3 infections. The period on the first plant is not included in the retention of the virus since the adults were able to acquire the virus again. Eleven adults induced only the initial infection.

**Attempts to Transmit the Viruses of Curly Top and Pierce's Disease of the Grapevine.** Because of the interest in curly top and Pierce's disease of the grapevine, attempts were made to transmit these by means of *Colladonus commissus.*

There was no proof that *Colladonus commissus* could transmit the curly-top virus to healthy sugar-beet seedlings or the virus of Pierce's disease of the grapevine to healthy wild grapevine seedlings. Some of the beet seedlings showed cleared veinlets on a portion of a leaf, a reliable symptom of curly top; but noninfective beet leafhoppers failed to recover the curly-top virus from such plants.

## COLLADONUS MENDICUS (BALL)

*Colladonus mendicus* (Ball) (= *Thamnotettix mendicus* Ball) has not been demonstrated to be a vector of California aster-yellows virus. One lot of 32 adults collected on creek nettle, *Urtica gracilis* var. *holosericea* on October 27, 1942, was kept on diseased celery for 19 days, and then 2 lots of 5 and 15 adults that survived were changed to 2 healthy celery plants, without results. Another lot of 5 adults, captured on California blackberry, *Rubus vitifolius*, was fed on an infected celery plant for 34 days and then transferred to a healthy celery plant, but caused no infection. One lot of 10 adults collected on creek nettle was kept on a diseased aster for 11 days; 4 surviving adults, transferred to a healthy celery plant, caused no infection. The longevity of the adults on healthy celery was only 4 days.

*Colladonus mendicus* was parasitized by a new species of Pipunculidae, described as *Allomethus oleous* Rapp (1943).

## COLLADONUS FLAVICAPITATUS (VAN DUZEE)

*Colladonus flavicapitatus* (Van Duzee) (= *Thamnotettix flavicapitatus* Van Duzee) (plate 1, *E, F*), collected on wild gooseberry, *Ribes* sp., in General Grant Park (DeLong and Severin, 1947) was usually parasitized by a species of Pipunculidae. The parasite was not reared. The leafhoppers were killed by the parasite before the virus incubation period in the insects was completed; this happened with 39 adults collected on September 15, 1944.

The transmission of the virus by this species of leafhopper was limited to three tests. One adult, after 11 days on a diseased celery plant, was changed to 3 successive celery plants at irregular intervals of 11 to 36 days and caused 2 infections. A single male was kept on an infected celery plant for 19 days and then on a healthy celery plant during adult life, but failed to produce an infection. One lot of 10 adults was kept on an infected celery plant for 17 days and then transferred to 5 successive healthy celery plants; 2 infections resulted.

## FRISCANANUS INTRICATUS (BALL)

*Friscananus intricatus* (Ball) (plate 1, *G, H, I*) is rare on the host plants recorded in the companion paper by DeLong and Severin (1948); but although low populations of leafhoppers were used, transmission of the virus to healthy celery was obtained.

Twenty males and females tested singly caused 3 infections (table 9). Two lots of 3 and 4 adults collected during the summers of 1943 and 1944 were kept on diseased celery from 11 to 12 days, and then were transferred to 4 and 13 successive healthy celery plants, respectively; 6 infections resulted—

35 per cent. The longevities of the last surviving adult in the two lots on healthy celery were 67 and 93 days, respectively, or an average of 80 days.

No transmissions from infected to healthy asters were obtained with 3 males and 1 female tested singly (table 9).

TABLE 9

TRANSMISSION OF VIRUS TO CELERY AND ASTERS BY VARYING NUMBERS OF *Friscananus intricatus*

| Plant and number of adults in each lot | Number of lots | Plants inoculated | Plants infected | Per cent infected |
|---|---|---|---|---|
| Celery: | | | | |
| 1 male | 6 | 6 | 1 | 17 |
| 1 female | 14 | 14 | 2 | 14 |
| 3 males | 1 | 4 | 0 | 0 |
| 4 females | 1 | 13 | 6 | 46 |
| Aster: | | | | |
| 1 male | 3 | 3 | 0 | 0 |
| 1 female | 1 | 1 | 0 | 0 |

TABLE 10

TRANSMISSION OF VIRUS TO CELERY AND ASTERS BY VARYING NUMBERS OF *Friscananus rupinatus*

| Plant and number of adults in each lot | Number of lots | Plants inoculated | Plants infected | Per cent infected |
|---|---|---|---|---|
| Celery: | | | | |
| 1 male | 50 | 50 | 15 | 30 |
| 1 female | 50 | 50 | 14 | 28 |
| 5 males | 3 | 3 | 1 | 33 |
| 5 females | 2 | 2 | 1 | 50 |
| 10 males | 1 | 1 | 0 | 0 |
| 15 males | 1 | 9 | 2 | 22 |
| 15 females | 1 | 12 | 0 | 0 |
| 15 males | 3 | 3 | 2 | 67 |
| 15 females | 6 | 6 | 2 | 33 |
| Asters: | | | | |
| 1 male | 8 | 8 | 0 | 0 |
| 1 female | 25 | 25 | 0 | 0 |

## FRISCANANUS RUPINATUS (BALL)

Nymphs and adults of *Friscananus rupinatus* (Ball) (= *Thamnotettix rupinatus* Ball) (plate 1, *J*, *K*) were collected on bracken, *Pteridium aquilinum* var. *lanuginosum*. Fifty males and 50 females, tested singly on healthy celery plants, produced 15 and 14 infections, respectively (table 10). The transmission of the virus to healthy celery by lots of 5, 10, and 15 adults is shown in table 10. Nine lots of 15 males or females kept on healthy celery plants during adult life transmitted the virus to 4 of 9 plants. During the summer of 1943, 1 lot of 15 males, after feeding on infected celery for 19 days, was transferred to 9 successive celery plants and caused 2 infections. During the summer of 1944, 1 lot of 15 females was kept on diseased celery for 12

days and then was changed to 12 successive healthy celery plants, but no infection resulted. The longevities of the last surviving adult in the two lots on healthy celery were 41 and 110 days, or an average of 76 days.

Eight males and 25 females, after feeding on infected asters 10 days or longer, were transferred to healthy asters and kept on them during adult life; but no infection occurred (table 10).

An attempt was made to transmit the curly-top virus by means of *Friscananus rupinatus*. Ten lots of 5 or 10 males or females were exposed to curly-top beets for a few days and then each lot was transferred to a healthy beet. All beets remained healthy.

## FRISCANANUS RUPINATUS VAR. BRUNNEUS DE LONG AND SEVERIN

*Friscananus rupinatus* var. *brunneus* DeLong and Severin (plate 1, *L*) was collected on bracken. Its efficiency in transmitting California aster-yellows virus was determined with single adults, each transferred from a diseased to a healthy celery plant. Infections were produced by 3 of 10 males, or 30 per cent; and by 11 of 50 females, or 22 per cent. As compared with these percentages, 50 males and 50 females of *Friscananus rupinatus* kept singly on healthy celery infected 30 and 28 per cent, respectively (table 10).

## SUMMARY

Evidence is presented in this paper that the following leafhoppers in the *Thamnotettix* group are vectors of the California aster-yellows virus:

*Idiodonus heidemanni* (Ball)
*Idiodonus kirkaldyi* (Ball)
Geminate leafhopper, *Colladonus geminatus* (Van Duzee)
Mountain leafhopper, *Colladonus montanus* (Van Duzee)
*Colladonus commissus* (Van Duzee)
*Colladonus flavocapitatus* (Van Duzee)
*Friscananus intricatus* (Ball)
*Friscananus rupinatus* (Ball)
*Friscananus rupinatus* var. *brunneus* DeLong and Severin

TABLE 11

SUMMARY OF RESULTS ON EFFICIENCY OF LEAFHOPPER SPECIES IN TRANSMITTING VIRUS, EACH VECTOR TESTED SINGLY ON HEALTHY CELERY OR ASTERS

| Species of leafhopper | Number of lots | Celery | | | Asters | | |
|---|---|---|---|---|---|---|---|
| | | Plants inoculated | Plants infected | Per cent infected | Plants inoculated | Plants infected | Per cent infected |
| *Idiodonus heidemanni* | 100 | 100 | 16 | 16 | 125 | 13 | 13 |
| *Idiodonus kirkaldyi** | 100 | 100 | 0 | 0 | 25 | 0 | 0 |
| *Colladonus geminatus* | 200 | 200 | 5 | 3 | 300 | 0 | 0 |
| *Colladonus montanus* | 100 | 100 | 11 | 11 | 100 | 0 | 0 |
| *Colladonus commissus* | 100 | 100 | 38 | 38 | 9 | 0 | 0 |
| *Colladonus flavicapitatus* | 2 | 4 | 3 | 75 | .. | .. | .. |
| *Friscananus intricatus* | 20 | 20 | 3 | 15 | 4 | 0 | 0 |
| *Friscananus rupinatus* | 100 | 100 | 29 | 29 | 33 | 0 | 0 |
| *Friscananus rupinatus* var. *brunneus* | 60 | 60 | 14 | 23 | .. | .. | .. |

* Infection was obtained with multiple lots.

A summary of results on the efficiency of each leafhopper species in transmitting the virus when tested singly on healthy celery or asters is given in table 11.

Celery is more readily infected than asters. The number of leafhoppers and the period of exposure to healthy plants plays an important role in the transmission of the virus to celery plants.

The latent period of the virus in 1 male of the geminate leafhopper, *Colladonus geminatus,* was 31 days. The minimum latent period in 11 lots of 100 males ranged from 11 to 36 days. In the mountain leafhopper, *C. montanus,* the minimum latent period in 10 lots of 100 adults ranged from 8 to 40 days.

The retention of the virus by 1 male *Idiodonus heidemanni* was 11 days after producing the initial infection; 2 males and 2 females each caused infection only in the first celery or aster. In tests on the retention of the virus with the mountain leafhopper, *Colladonus montanus,* 2 males and 1 female produced only the initial infection. One female of *C. commissus* retained the virus for 6 days and produced 3 infections. Eleven adults induced only the initial infection.

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Plate 1.—Color patterns which usually distinguish species of leafhoppers in *Thamnotettix* group, vectors of California aster-yellows virus: *A*, male, and *B*, female, *Idiodonus kirkaldyi* (Ball); *C*, male, and *D*, female, *Colladonus commissus* (Van Duzee); *E*, male, and *F*, female, *C. flavocapitatus* (Van Duzee); *G*, male, and *H*, *I*, females, *Friscananus intricatus* (Ball); *J*, male, and *K*, female, *F. rupinatus* (Ball); *L*, *F. rupinatus* var. *brunneus* DeLong and Severin.